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The development of the imbedded antheridium in Dryopteris stipularis (Willd.) Maxon and "Nephrodium molle"*

CAROLINE A. BLACK

(WITH PLATES 26–28)

The discovery by Farmer and Digby ('07) of the development of a sporophyte from the essential fusion of two vegetative cells of the gametophyte has aroused a keen interest in the study of apogamy in ferns and other higher plants as well, and has given a somewhat different meaning to the already variously interpreted term, apogamy.

These authors have found that in the prothallia of *Lastrea pseudo-mas*, var. *polydactyla* Dadds, and *Lastrea pseudo-mas*, var. *polydactyla* Wills, developed from normal spores and therefore possessing the gametophytic number of chromosomes, a doubling of the chromosomes was secured in an apogamous embryo by the migration and fusion of vegetative nuclei. The region of migrating nuclei, while not confined to a definite area on a prothallium, was always found to be in the younger portions. The basis of the entire process of the migration and fusion of nuclei was observed to be chemotactic. The elongated migrating nucleus coming in contact with the wall of the receptive cell was seen to slip through an opening, made, probably, by a fermentative action, and fuse with the nucleus of the invaded cell directly or after some time. It is believed by Farmer and Digby that this fusion of the nuclei of adjacent vegetative cells, accompanied by the doubling of the

* *Nephrodium molle*, according to Christensen (Index Filicum 444. 1905), is a synonym of *Dryopteris parasitica*.

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number of chromosomes, takes the place of the normal sexual fusion of the two gametes.

In addition to the above, the following ferns were studied: *Athyrium Filix-foemina*, vars. *clarissima* Bolton, *clarissima* Jones, and *unco-glomeratum* Stansfield; *Lastrea pseudo-mas*, var. *cristata apospora* Druery; and *Scolopendrium vulgare* var. *crispum Drummondae*. From these five forms, being aposporous, naturally or induced, there resulted prothallia having the double or sporophytic number of chromosomes. Different types of sporophytes were produced from these aposporous prothallia, namely: from the prothallia of *Athyrium Filix-foemina*, var. *clarissima* Bolton, and *Scolopendrium vulgare*, var. *crispum Drummondae*, the embryo arose in each case from an egg-cell, fecundation being unnecessary as the egg-cell already possessed the full complement of chromosomes. While the complete details were not made out for the origin of the embryo produced in *Athyrium Filix-foemina*, var. *unco-glomeratum* Stansfield, the probabilities are that it is like the preceding. The two remaining forms are examples of sporophytic budding. In *Athyrium Filix-foemina*, var. *clarissima* Jones, the sporophyte appears as the direct outgrowth of the apical surface in connection with an endogenous foot. The sporophyte in *Lastrea pseudo-mas*, var. *cristata apospora* Druery, makes its appearance as a small excrescence directly behind the growing point.

Lang ('98) presented a detailed account of the grosser phenomena of apogamous sporophytic outgrowths from prothallia grown from spores. The following fourteen forms are described: *Aspidium aculeatum* Sw., var. *multifidum* Woll., *A. angulare* Willd., var. *foliosum multifidum*, var. *acutifolium multifidum* (no results), *A. frondosum* Lowe; *Athyrium nipponicum* Mett., var. *cristatum*, *A. Filix-foemina* Bernh., var. *percristatum* Cousens, var. *cruciato-cristatum*, var. *coronatum* Lowe; *Nephrodium dilatatum* Desv. var. *cristatum gracile*, *N. Oreopteris*, var. *coronans* Barnes; *Polypodium vulgare* L., var. *grandiceps* Fox; *Scolopendrium vulgare* Sm., var. *ramulosissimum* Woll., var. *marginale*. His results were obtained from experimental cultures of prothallia, watering them only from below and exposing them to bright sunlight, diminishing in this way the frequency of fecundation. The most usual type of sporophytic budding cited in his paper is that of the

continuation of the prothallium as a cylindrical process. This process continues as a leaf or bears upon it leaves, roots, and ramenta. Sporophytic growths occur also on prothallia without the intervention of a cylindrical process, or as tracheids in the prothallium or cylindrical process. Sporangia also were observed to occur on the process.

Quite recently a paper has been published by Yamanouchi ('08, III) on apogamy in *Nephrodium*. This details an account of an embryo produced apogamously, with the gametophytic or x number of chromosomes. The writer in his previous papers on Sporogenesis and on Spermatogenesis, Oogenesis, and Fertilization in *Nephrodium* showed that under ordinary conditions the life history of this fern was quite orthodox. Under somewhat artificial cultural conditions, *e. g.*, keeping the prothallia rather dry and exposed to bright sunlight, watering only from below, fertilization was prevented. According to Yamanouchi the prothallia grown under such conditions developed slowly with larger cells than those grown under normal conditions. Antheridia were produced in abundance with active sperms, to all appearances capable of fertilizing an egg-cell, and reacting positively to 0.01 per cent. solution of sodium malate (*loc. cit.* 298). The rarely found archegonia were seen to be in a collapsed or poorly developed condition, probably incapable of functioning. The development of the sporophytic outgrowth was observed to be simultaneous with the growth of the archegonial cushion and to originate from a superficial cell in this region, in connection with cells just below it. No migration or fusion of nuclei was observed. The cells that comprise the apogamous embryo are distinguished from the cells of the prothallium by their smaller size, their relatively larger nuclei and denser cytoplasm. There is described here an embryo with the gametophytic number of chromosomes, arising from a single superficial cell and the vegetative cells beneath it, differing only in appearance from a normal embryo by the absence of the foot. This is the first case recorded of an apogamous embryo with the alleged gametophytic number of chromosomes.

During the autumn of 1908 several fine specimens of a southern fern,* *Dryopteris stipularis* (Willd.) Maxon, which were being

* The original specimen was brought from Cuba by Prof. C. H. Eigenmann.

grown in the greenhouse of the botanical laboratory of Indiana University, were placed at my disposal, with the suggestion that a study of the embryology be made with the view of ascertaining whether apogamy existed or could be induced in this species. Through the kindness of Mr. Alois Frey, a number of fruiting fronds of "*Nephrodium molle*" were obtained from the Lincoln Park Gardens, Chicago, from which cultures were also made and the prothallia studied in regard to the same problem.

METHOD OF CULTURE

Spores were sown upon sterilized soil in shallow earthen saucers. These were then placed in larger saucers of about the same depth. The cultures were watered with just enough distilled water after the spores had germinated to allow the prothallia to grow slowly. Water poured into the outer dish soaked up very slowly through the inner dish into the soil. This regulated the rapidity in the absorption of water by the soil and prevented the cultures from being alternately dry and moist. Evenness of moisture in the soil was further effected by placing a bell jar upon small blocks of wood, about one inch and a half high, above each culture. This allowed free circulation of air around the culture. This method prevented the collecting of moisture upon the dome of the bell jar and falling upon the culture, thereby making fertilization possible. The bell jars further protected the cultures from spores of fungi, etc. The prothallia grown under such conditions grew slowly but thrivingly. A glance at a culture presented the picture of a deep green carpet; closer inspection revealed the prothallia to be large, much larger than those, on which, under normal culture, embryos appear. No sporophytes occurred on the prothallia grown under these conditions. Material was fixed from time to time in chrom-osmic acetic and chrom-acetic acids. Prothallia were washed, dehydrated, and imbedded in paraffin. Sections were cut 5 and 6 microns in thickness and stained in safranin, Bismarck brown, and gentian violet. A detailed account of observations on each fern will now be given.

I. DRYOPTERIS STIPULARIS (Willd.) Maxon

Upon examining the sections, the prothallia were found to be unusually large. The archegonial cushion presented, in most

cases, a thickness twice as great as that of the normally grown prothallium; the apical sinus consisted of a large number of apical cells as seen in the consecutive sections of a prothallium. The wings were correspondingly large and somewhat wavy-margined. The entire prothallium, not having its period of functioning and usefulness ended by the production of a sporophyte, appeared overgrown in all directions. Archegonia and antheridia were produced on the upper as well as the lower surface. It is in the actively growing portion of the prothallium, *i. e.*, the vicinity of the apical sinus that one would look for some manifestation of apogamy. Well up in this region of the prothallium a structure was seen in a position to suggest an apogamous embryo, but this proved to be an imbedded antheridium (*figure 7*). Normal, as well as one or more imbedded, antheridia were found on the same prothallium. The initial cell of an imbedded antheridium is not distinguished in any way from the initial cell of an archegonium. The first wall laid down in the development of an archegonium is a periclinal one cutting off the initial cell of the neck. In a deep-seated antheridium the first division is likewise periclinal. The outer or superficial cell forms the cover, while the inner cell gives rise to the spermatogenous tissue. In all cases thus far observed, the second division of the inner cell of such an antheridium is an oblique one (*figure 1*). The resulting cells in this instance were unequal. In other cases, the division, also oblique, resulted in more nearly equal cells, as in *figure 2*. The nuclei in these cells were large, the cytoplasm dense and granular, and in staining characteristics typical of cells in young archegonia or antheridia. Three almost equal cells are seen in a developing antheridium in *figure 3*. Further divisions now take place in three planes until the structure becomes quite massive (*figures 4–7*). In *figures 5* and *6*, the identity of the structure is shown in its shrinking away from the surrounding cells. The proximity of these developing imbedded antheridia to the apical region is seen in *figures 1, 2, 4, 5*, and *6*. In *figure 7* is pictured the most typical form of a deep-seated antheridium. This is globular, projecting slightly above the surface of the prothallium. As the antheridium nears maturity the tendency to bulge outward is more pronounced. In the earliest stages the antheridium is usually even with the surface of the pro-

thallium, and it may remain so when mature (*figure 9*). *Figure 8* shows a form of antheridium occasionally met with. There is here a slight projection above the surface of the prothallium. This antheridium is peculiar in that it extends so deeply into the prothallium.

There seems to be no definite method for the further divisions of the outer cell. In sections, two or more cells are seen in the cover, irregular in size and depth. From this it will be seen that there is no definite arrangement or number in the cells comprising the cover. In most cases the antheridium was situated under one layer of cells, occasionally under two layers (*figure 10*). There was a marked variety in the size of imbedded antheridia. All degrees of size and shape were found from those about as large as the superficial type and rather globular to those more than twice as large and very irregular in shape (*figures 7–9*). The finding of imbedded antheridia upon these prothallia was not an occasional thing but a common occurrence, the majority of the prothallia grown under the above-detailed conditions bearing one or more imbedded antheridia. As a rule these were found upon the largest prothallia, although occasionally one was seen on a smaller prothallium. These deep-seated structures were always found to be in the apical region or within a few cells of it.

Typical of cell divisions in normal antheridia, the cells in the imbedded type divide simultaneously. The development of the sperms in the imbedded antheridium was followed closely and was found to differ in no way from that of the sperms in normal antheridia, a sperm from an imbedded organ appearing exactly like a sperm from a superficial one. Owing to the occurrence of both normal and imbedded antheridia on the same prothallium and the similarity between the sperms, sperms from a deep-seated antheridium could not be isolated.

In *figure 11* is seen a section of a prothallium immediately back of the apical region, in which are two imbedded antheridia and a normal archegonium. More than one half of the antheridium, the lower one in the figure, consists of sperm mother-cells, the rest of the antheridium being made up of four large cells. These cells have the granular cytoplasm characteristic of developing sex-cells. Another case similar to the foregoing was observed (*figure 10*),

in which instance the antheridium, also in the apical region, was imbedded under two layers of cells. Approximately half of this antheridium consisted of mature sperms, the other half, that nearer the surface, was composed of three cells, two smaller and one very large with a corresponding large nucleus. This last cell bore a striking resemblance to an egg-cell.

The development of the imbedded antheridium is very similar to that of the antheridium in a lower order of ferns as described by Campbell ('07) in the Ophioglossaceae, with the exception of the first divisions and the development of the cover-cell. An approach to the imbedded antheridium of *Dryopteris stipularis* and "*Nephrodium molle*" is found in the antheridium of *Ceratopteris* (Engler & Prantl, Nat. Pflanzenfam. '02). This antheridium projects but slightly above the surface of the prothallium, although it has the customary lid- and ring-cells. The basal cell, assuming a more irregular shape, is designated as the pedicel-cell.

II. "NEPHRODIUM MOLLE"

The origin of the imbedded antheridium in "*Nephrodium molle*" is similar to that of an archegonium and not unlike that described for *Dryopteris stipularis*. After the first division of the initial cell into the outer and inner cells, the inner cell divides periclinally into two unequal cells (*figure 12*), recalling the development of an archegonium. If a division of the larger cell should take place obliquely, a condition would be found as shown in *figure 13*. Further divisions of the two inner cells give rise to the condition seen in *figure 14*. That such structures would develop into imbedded antheridia seems positive. The structure shown in *figure 24*, for example, may have originated in a manner similar to that of an imbedded antheridium, but it is certain that none of these structures would become sporophytes.

These developing structures found in the apical portion of the prothallia will be seen to be similar to the early stages in the development of the imbedded antheridium of *Dryopteris stipularis*. *Figure 14* in "*Nephrodium molle*" could represent an early stage in the development of *figure 8* in *Dryopteris stipularis*. The cells in these structures differ markedly from the surrounding cells in their granular cytoplasm and large nuclei. In *figures 12–14*, the

nuclei of the cover-cells have recently divided, whereas the nuclei of the inner cells are in a resting stage. A typical imbedded antheridium similar to those found in *Dryopteris stipularis* is seen in *figure 15*. It projects slightly above the surface now but probably did not in its earlier stages. Three cells of the cover are shown in the section. The developing sperms are quite normal, the cells having rounded up, with the blepharoplast showing plainly in some of them. As was the case in *Dryopteris stipularis*, both kinds of antheridia appear on the same prothallium. In some cases an imbedded antheridium will be seen very near a superficial one. In *figure 16*, a small imbedded antheridium is seen adjoining one of the superficial type. There is a slight variation in the basal cell of this last antheridium, inasmuch as it has redivided until it consists of at least three cells. In the imbedded antheridium are a few almost mature sperms, lying loosely in the antheridial cavity. Two very narrow cells are at the base of this antheridium. It is very often the case that some of the cells immediately surrounding the antheridium are narrow. An antheridium, which had a deep-seated origin but in its development projected considerably above the surface of the prothallium, is pictured in *figure 17*.

Figures 18 to *24* comprise a series of drawings from consecutive sections of one prothallium. There are three structures here whose origin is similar to three adjacent archegonia. In *figure 18* two cells with the superficial or cover-cell are seen. The wall separating these two cells is diagonal, recalling a similar condition in *Dryopteris stipularis* (*figure 2*). This in itself is an irregularity for the normal division of an archegonium initial. The next section (*figure 19, a*) shows the same two cells; the innermost cell is a little the larger as is seen in the successive sections. This first structure contains, in all, four cells (*figures 21–23*). The other two cells are also divided by a diagonal wall, the position of this wall being at right angles to the wall separating the first two cells. The wall dividing the two pairs of cells is in the plane of the page. The beginning of the second structure is seen in *figure 19, b*. It appears here as a little hump of three cells, part of the cover. The next section (*figure 20, b*) shows that beneath this cover are two cells, one projecting up into the little hump. In *figure 21, b*,

these cells are seen plainly with their large nuclei. The similarity between this and the two-celled stage of an archegonium is striking. Below these two cells in the second structure (*b*) are three more cells (*figures 21–23, b*). In these three cells, of which all three nuclei are seen, one cell is superimposed on the one below, the two nuclei appearing one above the other. The wall of the third cell is indicated by the dotted lines. The second structure (*b*) consists therefore of five cells, lying beneath a cover which arches slightly upward.

The third structure (*c*) is first seen in *figure 21, c*. Three small cells here project slightly at the left of the second structure (*b*). The next section (*figure 22, c*) shows this projection, corresponding to the neck of an archegonium, to be much larger. In this figure are seen three cells belonging to the third structure. The cells of the three formations are seen here (*figure 22*) to lie together as one mass of actively growing cells. From their position in the apical region of the prothallium and from their dissimilarity to the surrounding cells, *i. e.*, their granular, densely staining cytoplasm, large nuclei and absence of chloroplasts, these structures undoubtedly came from potential sex-cells. *Figure 23, c*, shows a section cut through the so-called neck of the third structure. Two small cells are seen in the neck-like projection, beneath which are three cells (*figures 23, 24, c*). Below these three cells are two more, making a total of nine in this structure (*figure 24, c*). The character of these last two cells justifies the opinion that this structure is of archegonial origin. The two cells mentioned seem to correspond to an egg- and ventral canal-cell of an archegonium.

The cultures of "*Nephrodium molle*" presented the same general characteristics as those of *Dryopteris stipularis* grown under these conditions, differing only in the rapidity of growth, these prothallia not growing quite so slowly as those of *Dryopteris stipularis*. No apogamous sporophytes were found on these prothallia.

GENERAL CONSIDERATIONS

From the foregoing description of the structures obtained through varying the normal cultural conditions, it will be seen that the prothallia of *Dryopteris stipularis* and "*Nephrodium molle*"

present a remarkable mobility. As dryness and the exposure to direct sunlight were the only cultural changes from the normal state, the results obtained may be attributed to those causes, none of these structures being found in the normal control cultures. The fact that one form of the expression of the potentialities of these prothallia is that of a deep-seated antheridium is of interest from a number of standpoints. Morphologically the imbedded antheridium is interesting, in that its origin and development is very similar to the origin and development of the normal antheridium of a much lower order of ferns. The detailed development of the antheridium in the Ophioglossaceae (Campbell '07) is essentially similar to the development of the imbedded antheridium as found in *Dryopteris stipularis*. The position of these antheridia in the actively growing part of the prothallium is evidence of the manifestation of an active response to a forced environment and not a condition due to degeneracy or a reversion to more primitive characters. The presence of normal antheridia on the same prothallium bearing the imbedded kind shows that, while the conditions are equal for producing either, the condition of dryness is essential for the formation of the deep-seated antheridium. The imbedded antheridium in the dry cultures was not an occasional occurrence, as one and frequently two or three were found on the majority of the prothallia.

That the response to this dry condition was the production of imbedded antheridia, shows the far-reaching effect of such an environment, as well as the success of the prothallia in combating it. A superficial organ on a prothallium grown in dryness is more in danger from drought than one deeper in the prothallial tissue. To protect the antheridia from the disasters of drying out and thus becoming incapable of functioning, an antheridium has been developed, completely imbedded in the prothallium. Deep seated in its origin and development, such an antheridium is protected from the effects of drought, obtaining from the surrounding prothallial cells the maximum amount of moisture supplied the plants. The improbability of a sperm from a superficial antheridium reaching an egg is apparent in these prothallia due to the lack of the necessary medium, *i. e.*, water. If there could be an internal way for the sperm to reach an egg, another suggestion of

the meaning of the imbedded antheridium would be evident. If the migrating and fusing nuclei, producing the apogamous embryo as described by Farmer and Digby, could be traced to such sexual elements as might mature into a deep-seated antheridium or an archegonium, the adaptation there would be more complete. The morphological position of an imbedded antheridium, then, can be regarded as only the expression of the potentialities of the plant, one evidence of the response to environmental conditions.

The sperms from either antheridium apparently differ in no particular. There was a greater variation in the number of sperms in the imbedded antheridia than in those of the normal type, the imbedded antheridia being larger on the whole than the superficial ones. The individuality of the deep-seated antheridium is shown in its slight shrinkage from the surrounding cells.

The case of the imbedded antheridium in which half consists of mature sperms and the other half of three large cells, one resembling very much an egg-cell (*figure 10*), presents another standpoint from which these structures may be considered. This is the subject as to the determination of sex. The question arises, has any cell of a prothallium destined to be a sex-cell the potentialities of either sex? When we remember that these are monoecious prothallia, that each cell came from a spore and that all spores are alike, it would seem as if there were some basis for such a supposition. If we accept this supposition as true, the earliest stages of the imbedded antheridium may be interpreted as the earliest stages of an archegonium. After the first division of a superficial cell into an inner and an outer cell, the inner cell instead of developing into an archegonium becomes the initial of a deep-seated antheridium. The origin of the case above cited may then be explained as a sex-cell, the potentialities of either sex being almost equal, so that half of the structure consists of sperms or the male element, and the other half, composed of three cells, one especially resembling an egg-cell, represents the female element.

Another case, the lower antheridium in *figure 11*, is shown where more than one half of the structure consists of sperm mother-cells, the rest of the antheridium being taken up by a number of large cells, which may represent the female element of the original cell. The fact that maleness dominates in these structures and that imbedded

antheridia are the result of dryness and not abortive archegonia, may be due to the amount of moisture supplied. In dioecious ferns the archegonia are found on the larger prothallia, the antheridia on the smaller. Good cultural conditions may favor the probability of a destined sex organ, female; poor cultural conditions, male, although experimental evidence is conflicting on this point.

While the data are not so complete for "*Nephrodium molle*" as for *Dryopteris stipularis*, less material of the former having been prepared and studied, the origin of the imbedded antheridium found in this fern is undoubtedly similar to that of *Dryopteris stipularis*. That the structures seen in *figures 12–14* would develop into imbedded antheridia can not be definitely stated, but that deep-seated antheridia could originate in this manner is certain. A more exhaustive study of both ferns may bring out more facts. Normal antheridia, imbedded antheridia, and a transitional stage (*figure 11*) where an antheridium had a deep-seated origin but in its development projected beyond the surface of the prothallium, were all found in "*Nephrodium molle*."

The condition represented in *figures 18–24* is a different expression of "*Nephrodium molle*" under a dry state. The origin of the structure (*c*) in *figures 22–24*, at the base of which are the apparent egg- and ventral canal-cell, is without question a cell which under normal conditions would have given rise to a normal archegonium. The impossibility of this egg being fertilized, due to its position and the improbability of a sperm being attracted to it, is obvious. What the other two structures would give rise to is unknown. That they might produce egg-cells is a possibility, or that they might become imbedded antheridia is also to be considered.

It is impossible to draw any parallel between the imbedded antheridium of these ferns and the antheridium of *Ceratopteris*, the latter being borne on an aquatic fern, and structurally similar to the ordinary antheridium.

No apogamous sporophytes were found in the cultures of either fern. In anticipating the production of apogamy in these ferns, a type of sporophyte was expected similar to that described by Lang, *i. e.*, sporophytic budding from the prothallium or upon a process from the prothallium. If the sporophytes produced from the spore-grown prothallia of Lang do not originate from vegetative

fusion of nuclei, their life history, as far as the number of chromosomes is concerned, is similar to the life history of the apogamous "*Nephrodium molle*" described by Yamanouchi. The figures of Yamanouchi, illustrating the development of this apogamous embryo, are not convincing. There is no evidence that the shaded cells in his figure 1 (*loc. cit.* 299) develop into the embryo shown in figure 29 (*pl. 10*). If apogamy is present in "*Nephrodium molle*," this plant shows greater potentialities than *Dryopteris stipularis* at the present time. A study of just how much dryness will cause the development of imbedded antheridia and how much will bring forth apogamy seems desirable.

While the main object in carrying on this investigation, namely, to obtain apogamy, has not been accomplished, an antheridium has been found that, so far as the writer knows, has not been obtained before. Acknowledgment is due here to the courtesy of Professor D. H. Campbell, who confirmed the above opinion as to the newness of such an imbedded antheridium in the higher ferns.

I wish to express my deep gratitude to Dr. David M. Mottier for his constant advice and encouragement throughout this study.

CONCLUSION

At the present time I have found no apogamy in either *Dryopteris stipularis* or "*Nephrodium molle*," although, as far as I was able to determine, the cultural conditions described by Yamanouchi were repeated. An imbedded antheridium similar to the antheridia of lower ferns was found on the majority of the prothallia of *Dryopteris stipularis* and on a number of the prothallia of "*Nephrodium molle*." In *Dryopteris stipularis*, in addition to imbedded antheridia, deep-seated structures were found, half of which consisted of sperms and the remainder of large cells. In "*Nephrodium molle*" a deep-seated egg- and ventral canal-cell were found.

INDIANA UNIVERSITY,
BLOOMINGTON, INDIANA.

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Explanation of figures in plates 26–28

All figures were drawn with the aid of a camera lucida, using homogeneous oil-immersion objective 2 mm. combined with ocular 4.

1–11. *Dryopteris stipularis*

1. Two-celled stage of an imbedded antheridium in the apical sinus.

2. Similar stage as above, the antheridium projecting slightly above the surface of the prothallium. The two cells are more equal in size.

3. Three-celled stage of an imbedded antheridium.

4. Young stage in the development of an imbedded antheridium. Apical cell not shown.

5. Stage similar to that in fig. 4. Antheridium shows no projection from the prothallium.

6. Antheridium in the apical portion, showing slight shrinkage from the surrounding cells. Relative density of cells in antheridium and in the prothallium is seen. Figs. 1, 4, and 6 indicate the width of the cushion.

7. Globular imbedded antheridium, causing a slight mound on the surface of the prothallium.

8. Wedge-shaped antheridium projecting deeply into the prothallium. Cytoplasmic contents of cells beginning to round up.

9. Large mature antheridium, not projecting from the prothallium at all. Irregular outline of antheridium is seen.

10. Deep-seated antheridium in which only half has developed into sperms. The other half consists of three large cells, one, that nearer the surface, resembling an egg-cell. This antheridium is situated under two layers of cells. The cover of those pictured in figs. 1–9 consists of but one layer of cells.

11. Section showing two imbedded antheridia and a normal archegonium in the apical region. The lower antheridium in the figure consists partly of sperm mother-cells. The remainder is made up of four large cells.

12–24. *Nephrodium molle.*

12. A structure, similar to a young archegonium, which may be the beginning of an imbedded antheridium.

13. An older stage. This could represent a stage in the formation of an imbedded antheridium.

14. A five-celled, deep-seated structure similar to a step in the development of imbedded antheridia. The densely granular cytoplasm and large resting nuclei are indicated.

15. Imbedded antheridium, projecting slightly. Cells beginning to round up.

16. Small imbedded antheridium, with almost mature sperms, adjacent to a superficial one.

17. An antheridium of deep-seated origin, projecting half way above the surface of the prothallium.

18. Two cells under a cover-cell *a* of a deep-seated four-celled structure. This and the following figures are from consecutive sections of a prothallium.

19. The same two cells of structure *a* are seen. Three cells in the cover of structure *b* project slightly from the surface.

20. More cells of the cover of structure *a* are seen. The lower cell of the first pair is below this cover. In structure *b* there are two cells, one projecting up into the cover.

21. The beginning of the third structure *c* is indicated here by three small cells, part of the cover. Two cells of structure *b* show. In structure *a* the second pair of cells, with the wall dividing them at right angles to the wall dividing the first pair fig. 19, *a*, is seen.

22. The cells of three structures appear as one contiguous mass of actively growing cells. Both nuclei of the second pair of cells of structure *a* are present. In structure *b* three cells in addition to those already described are seen beneath them. The cover of structure *c* projects considerably above the surface. Only three cells of this last structure show.

23. Structure *a* presents about the same appearance as in the preceding figures. Two cells of structure *b* are visible. This section passing through the neck-like projection of structure *c* discloses two small cells in it. Beneath this are four cells.

24. The two lowest cells of structure *c* are seen to resemble strikingly an egg- and ventral canal-cell. Above this so-called ventral canal-cell, three cells appear, two of which were present in fig. 23, *c*. Structure *c* consists, then, of nine cells, running through figs. 21–24. The cells in these three structures differ from the surrounding cells in their granular contents and large nuclei.

Notes on the anatomy of Parosela spinosa (A. Gray) Heller

AMELIA RICHARDSON GOODLATTE

(WITH PLATE 29)

The synonymy of this plant is considerable and though the generic name *Parosela* of Cavanilles has priority, in the somewhat scanty literature on the species it usually appears as *Dalea*. It belongs in the order Papilionaceae under the tribe Galegeae. The species is distributed from Arizona northward to Colorado and the California desert and southward to Sonora and Lower California. In stature it is a small tree, sometimes attaining a height of 18–20 feet, with a short trunk and very numerous branches. It is densely spinose, the spines being apparently modified branches, and the older stems are covered with a rough scaly light brown bark. The younger portions, up to stems of the third year, are densely clothed with hairs, and both the stems and spines bear small epidermal emergences or scales, and a few leaf-buds. These, together with the numerous large glands which form noticeable brown spots and protuberances on the surfaces of spines, stems, and leaves, give a decidedly rough and lumpy appearance.

The hairs are of a single type ; each consists of two short basal cells and a long, pointed end-cell, the outer part of the walls being cutinized, especially in the basal cells, while the remainder is formed of unmodified cellulose. The small scales or epidermal emergences are conical in shape, hollow in the center, their walls formed of two or three layers of small, nearly cubical cells, the outer ones cutinized like the epidermis.

The system of branching proves to be one of the most interesting of the external features. The superficial appearance is almost that of a dichotomous branching, but investigation shows that in every case a branch arises from a leaf axil. The apparent confusion is due to the fact that the spines are really the main axis transformed, while the axillary shoot, continuing to grow, takes the place of the main axis and itself gives off a shoot, which, developing rapidly into another branch, in its turn gives rise to a

spine and a shoot. Thus, with very few exceptions, in the material examined, there was a regular alternation; first, an axillary shoot, becoming the axis, the main axis being arrested and developed into a spine, then a fork with both axis and shoot developing into equal branches, then again, on each of these a spine and a shoot, and so on. At the growing tip it can be seen that the transformation of axis into spine takes place at a very early stage, the tip becoming horny and the stereome tissue strongly developed before the shoot is well out of the enfolding leaf and considerably before the formation of the axillary shoot which is to take its place as axis.

The most striking internal characters are, in general, the great development in the stem of chlorophyl-bearing tissue to assume the functions of the fugacious leaves, the occurrence in great numbers of crystals of calcium oxalate, and especially the very general distribution and prominence of glands and secretory apparatus.

The leaves, as has been said, remain on the plant only a very short time, and are comparatively few, even in the season. The minute paired stipules each have a large, persistent gland at the base, of the same anatomical character as the glands which are scattered irregularly over the stem and leaf. The hairs cover both surfaces of the leaf, clustering most densely in an irregular arrangement around the stomata. Weyland finds it characteristic of the tribe of the Galegeae, almost without exception, that the stomata are surrounded by cells arranged without any special order, neighboring the guard cells. *P. spinosa* possesses this character in common with the rest of the tribe. The stomata occur on both surfaces of the leaf, but are more numerous on the under side. They are simple in type, the guard cells not being even deeply sunk, though their outer walls are heavily cutinized, in common with the other epidermal cells.

In addition to this layer of cutin, the epidermis of the leaf is noteworthy because of the occurrence of rhomboidal crystals of calcium oxalate in a few of its cells. In regard to the shape of the crystals found by him in the epidermis of the single species *Dalea versicolor* Zucc., Weyland describes them as being short and rod-shaped, the cells containing them lying either singly or in groups, and being smaller than the surrounding cells. In *P. spinosa*,

however, the crystals are distinctly rhomboidal and the small cells containing them are always single in the midst of the larger, ordinary cells (FIGURE 3).

Crystals, in greater or less numbers, in the accompanying tissue of the vascular bundles and in the palisade cells, Weyland finds to be a general character for the order, and he further states that those in the palisade cells are rod-shaped throughout the genus *Dalea*, while the rhomboidal form also occurs in some species. This proves to be true in the case of *Parosela spinosa*. In the layer of cells immediately under the epidermis, and in the mesophyl in general, these rhomboidal crystals are very numerous, especially in the cells surrounding the bundle-strands. The crystals in the palisade tissue are rod-shaped and sometimes partly imbedded in the cell-wall.

The further structure of the leaf is quite simple. It consists of palisade and spongy tissue, the leaf-edges being rolled so that the palisade cells extend round to the under side. The bundles are concentric, surrounded by a considerable layer of stereome tissue, and around that again, as has been mentioned before, a layer of cells with numerous crystals. Weyland cites the case of *Dalea polyadenia*, where these cells with crystal-complexes apparently take the place of bast-fibers as strengthening material, and it may very well be that in *P. spinosa* also they are of auxiliary use in giving rigidity to the leaf-bundles.

The secretory apparatus of the leaves can best be discussed in connection with that of the stem, as the anatomical character of the two is the same. The stem up to the third year has a highly developed chlorophyl-bearing tissue in the cortex, consisting of five or six rows of palisade cells. The stomata are of the same simple type as those of the leaves, being perhaps rather more deeply sunk, in a pit formed by the thickened outer walls. The epidermis has a heavy outer layer of cutin from a very early stage, and this increases until in the third year the entire outer wall, and the radial wall as well, are completely cutinized. As in the leaves, rhomboidal crystals are sparsely scattered through the epidermal cells. The hairs form a thick coating until the formation of the periderm supplants the primary cortex.

Sanio, speaking of periderm formation in general, states that

"Der Sitz der Korkbildung ist übrigens für jeden Species, ja man kann sagen Gattung, constant." Solereder, on the other hand, quoting as authorities Sanio, J. E. Weiss, and Douliot, on cork formation in the Papilionaceae, says that the position of the cork-forming layer differs not only within the limits of a genus but also "bemerkenswert ist, dass zuweilen bei derselben Art der Ort der Korkentstehung zwischen der zweiten und sechsten Zellschicht der primären Rinde wechseln kann." * Weyland finds that in *Dalea*, in the genus as a whole the cork is formed in the second to sixth cell-row of the cortex. In the plant under discussion it is formed, however, on the very inner row of the primary cortex, immediately outside the primary stereome bundles. This would be about the ninth or tenth row, as the number of rows of palisade cells is variable. Hence there is considerable variability in the genus in this respect (FIGURE 4).

A cross-section of a young stem shows, first, the epidermis, with a layer beneath it of cells containing rhomboidal crystals; then five or six rows of palisade cells, many of them containing rod-shaped crystals; then, a layer of parenchyma cells, with rhomboidal crystals; next, the row of collateral bundles and a cambial ring, rather ill-defined, each bundle being accompanied on the side toward the periphery of the stem by a strand of primary stereome tissue. In the center, of course, are the pith cells, with rather thickened walls, some of them transformed into tracheidal parenchyma with simple pores, and many of them, especially those nearest the wood, containing rhomboidal crystals, sometimes in the cell-cavity, sometimes imbedded in the wall. The only interruption in the simple regular character of the stem structure is the occasional appearance of a few cauline bundles, of the collateral type, accompanied by a stereome strand outside the leptome (FIGURE 5).

As the young stem develops, the layer of cutin, as has been remarked, becomes more strongly developed. When the cortex is supplanted by cork cells the outer ones of these have cutinized walls, the inner (phellogen) layer retaining unmodified cellulose walls. Traces of suberin appear in a few cells of the hadrome,

* Anat. Dicot. 313.

from the third year on. The crystals are increasingly numerous as the stem develops. Lignification begins, naturally, in the ducts and tracheids even of the very young stem, and proceeds as the plant grows older, through the walls of the primary stereome, the pith, the inner walls of the parenchyma cells lying next the primary bast bundles, the walls of the secondary stereome, of many scattered palisade cells, and finally occurs in the cells of the bark when this is formed in the sixth year. As the lignified areas increase, the areas containing walls of unmodified cellulose become reduced to those of the leptome, cambium, phellogen, and whatever remains of the palisade tissue. Starch is found from the first to the third year in the contents of the palisade, pith, parenchyma, and medullary ray cells. After this it disappears as the stem becomes less and less an assimilating organ. Proteids, likewise, occur in conjunction with the green tissue and decrease with it.

In the parts of the stem which become modified into spines the process of lignification takes place much more quickly than in the stem that continues to grow. In place of parenchyma cells a stereome ring fills the spaces between the hadrome masses of the bundles. This is especially noticeable as a point of difference between a very young spine and a very young shoot (FIGURES 1 and 2). After this rapid development of tissue that serves to give strength and rigidity, the growth of a spine is limited to simple thickening and enlarging, for there is no secondary thickening.

In the growing stem secondary thickening takes place according to the ordinary dicotyledonous type from a cambial ring. The sieve-tubes are comparatively short and wide. The vessels differ greatly as to size, but all have simple, oval pores, as is characteristic of the family. The walls of the smaller tracheids are spirally thickened. The medullary rays, as usual in the greater number of Papilionaceae, consist of about three cell-rows, somewhat increased toward the outer part in a wedge shape.

Solereder * quotes Saupe to the effect that the medullary ray cells of the Galegeae are small and round in tangential section. In this case, however, they prove to be oblong and almost rectangular. The wood-prosenchyma cells, where they come into contact with the ducts, have, like them, simple oval pores. There

* *Loc. cit.* 310.

are no distinct bundles of secondary bast, not in direct contact with the medullary rays and marked off by a distinct sheath. On the contrary, the secondary stereome is in direct contact with the medullary rays and with the wood. The masses are composed mainly of prosenchymatic or perhaps sclerenchymatic cells, while those of the bast type, with long, pointed ends, are mixed with them in small groups.

The secretory system is extremely well developed, all the varieties of internal secreting organs that are mentioned as occurring in the tribe being found in this species. (This does not include the glandular hairs possessed by a few Galegeae.)

The material used for this work was, first, a dried herbarium specimen which was soaked in a mixture of glycerine, alcohol, and water, to make cutting possible, and afterwards some branches that had been obtained in a living state, through the courtesy of Dr. D. T. MacDougal, but were preserved in the same mixture. Probably something in this method of preserving affected the secretions of the glandular tissues. At all events, all tests for determining their exact contents were unsatisfactory, so that the only conclusion to be obtained is that, since they are analogous in anatomical structure to the organs tested by other observers, their contents are presumably of the same nature.

Throughout the stem and spines there are strands of elongated cells with thin walls and a large cavity, sometimes lying singly, but more often two or three together, in the innermost layer of the primary cortex. In some cases they are immediately adjacent to the bundles of primary stereome, in others they lie opposite the medullary rays (FIGURE 5). Trécul found a similar set of cells with tannin contents in the cortex and also on the outer edge of the pith in *Dalea alopecuroides*. He describes them as "ces sortes de vaisseaux à tannin dont les cellules ne sont ordinairement pérforées." Baccarini describes similar ducts in many Leguminosae, which he says may appear in one stage of the plant's growth and disappear subsequently, or may be permanent. These tannin elements are situated: 1, around the pith and outside the stereome; 2, in the periphery of the pith, grouped around the vascular apex of the wood triangle of each bundle, and on the sides of the stereome; 3, around the pith, within the stereome and on its sides;

4, around the pith and within the leptome. These tannin elements are not of invariable occurrence, he finds, in the Leguminosae, and part of the tribe of the Galegeae is without them. *Dalea*, however, belongs to the series provided with this sort of secretion organ. These ducts contain in addition to tannin, he says, albuminous material which will stain bright yellow in iodine, although the tannin interferes somewhat with the reaction. Weyland verifies Baccarini's results in general, but finds that what he interpreted as a transitory appearance of tannin-bearing elements is due to the difference of the contents of the ducts at different stages. In the young stem the contents are almost wholly albuminous and the tannin appears later, which explains, he adds, the great size of the ducts relative to the amount of tannin contained.

In *Dalea*, Weyland observed these ducts in the pith, Trécul in the pith and the primary cortex as well. In the species under discussion, as far as the available material showed, they occur only in the cortex. As has been said, the tests to determine the contents were most unsatisfactory. The ducts were filled with a substance of red-brown color, and this of course made all those tests for tannin which depend upon a red or a brown color-reaction, unavailable. Copper acetate, iron sulphate, and iron acetate, which should give green, black, or blue color, had apparently no effect. It seems probable that the preserving liquid must have affected the contents in some way, although the liquid itself, when tested for tannin, showed no result, so that this could not have been extracted in any large quantity. The arguments, then, for considering these ducts as part of the albuminous-tanniferous apparatus similar to that of other members of the genus and tribe, are simply based upon the similarity in structure and position. The similarity in structure is at once apparent and that in position is evident when one considers Baccarini's statement that the cells normally lying on the sides of the bundles of hard "libro," are sometimes pushed out till they lie between the bundles.

Another type of secretory organ which is very prominent in *P. spinosa* is an ovoid schizogenous gland with an opening to the exterior through a small slit, and surrounded by a firm layer of close-set cells, which show traces of lignification, lined by a layer of papillary epithelium, with densely granular cell-contents, light

brown in color (FIGURE 6). Weyland speaks of finding only traces of this epithelium at an early stage in the formation of the gland, and says that it later breaks down and a schizogenous-lysigenous gland results. In the species *P. spinosa* this is not the case, as the epithelium is plainly marked even in a gland occurring on an old spine, where it is presumable that the gland is of a considerable age. It is glands of this type which form the lumps on the young branches, alluded to by Solereder, and which occur at the bases of the stipules. They occur in numbers in the palisade tissue of the primary cortex, but are naturally absent from the older branches on which the periderm has supplanted the cortical tissue.

In the attempt to decide on the nature of the contents secreted by these glands, we have again to record no result. In this case it would seem that the contents have been extracted. Weyland finds round glands of the same type in all the genera of the subtribe Psoraleae that he examined. They contained a light or dark yellow resin, which was soluble in alcohol. The occurrence of these glands with resinous contents is a character for divisions greater than a genus, he claims. Therefore, since glands of the same structure and position contain resin in other species of the genus and subtribe, and since the resin is soluble in alcohol, it seems safe to conclude that the contents were resinous and have been extracted by the alcohol in which the material was placed.

This completes the secretory apparatus of the stem. The leaves contain the same round glands, which appear in either the palisade or spongy tissue, opening toward either surface. No trace of tannin ducts nor of the single isodiametric tannin-secreting cells, nor of the layer of tannin cells in the mesophyl, mentioned by Baccarini as present in the group, could be found. In addition to the resin-bearing glands, however, the leaves contain a peculiar type of gland, the so-called intercellular glands. These are composed of elongated cells which have split apart from each other, so that in the mature gland they present the appearance of strands of tissue running through the cavity of the gland. Around the whole is a sheath of close-set cells, developed from the mesophyl (FIGURE 7). It is only in the mesophyl tissue and opening on the under side of the leaf that glands of this type occur. Their contents are small pieces of hardened brown stuff,

which is undoubtedly tannin but refuses to respond to any of the tests, like the tannin in the other cases. Solereder describes an exactly similar gland in *Psoralea*. It is the brown coloring of these glands which causes the noticeable brown spots on the leaves of dried material in this species.

This completes the survey of the anatomical characters of *Parosela spinosa* as far as they have been ascertained. The work was done under the direction of Dr. Herbert M. Richards, to whom thanks are due for his many kind suggestions and encouragement.

BOTANICAL LABORATORY,
BARNARD COLLEGE,
COLUMBIA UNIVERSITY.

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Explanation of plate 29

1. Stem in first year, showing distribution of main tissue areas. Chlorenchyma, stippled; stereome, black; vascular bundles indicated in outline. Magnified 12 diameters.

2. Spine in first year, as above, showing the greater development of the stereome. Magnified 12 diameters.

3. Surface view of epidermis of leaf. Magnified 250 diameters.

4. Periderm formation in stem of third year. Magnified 136 diameters.

5. Transverse section of portion of stem in third year. The vessels indicated by cross-hatching contain the dark brown albuminous substance. Magnified 136 diameters.

6. Gland in stem. Magnified 250 diameters.

7. "Intercellular" gland of leaf. Magnified 250 diameters.

The figures were all drawn with the aid of an Abbé camera, and the magnifications given above are $\frac{2}{3}$ of that of the original drawings.

Some coastal plain plants in the Piedmont region of Georgia

ROLAND M. HARPER

In the indigenous flora of North America there are several hundred species, perhaps more than a thousand, which, whatever their distribution may have been in prehistoric times, are now known only from the coastal plain. Up to a time within the memory of every living botanist the coastal plain was scarcely recognized by phytogeographers (I have found very few distinct references to it in botanical literature earlier than 1900), and the fact that so many species are endemic to it was therefore only dimly realized if at all. In the last two decades, since botanists have begun to pay more attention to plant distribution, many species formerly known only from the coastal plain have been found in the older regions farther inland; and this may have led some to believe that all species now supposed to be confined to the coastal plain will be found also outside of it when the country is more thoroughly searched. But at the rate that such discoveries are being made it would seem that the limit has almost been reached, and that there are still hundreds of species which do not (and probably never did) grow outside of the coastal plain.

Those species which are common in the coastal plain and rare elsewhere constitute an interesting though naturally not well-defined class, and it is chiefly through a study of these that we may hope to learn something of the origin and history of those of more restricted distribution above mentioned. It is impossible to say how many should be included in this class, since there is no sharp distinction between them and those species which are equally common in and out of the coastal plain on the one hand, and those now supposed to be confined to the coastal plain, but hereafter to be found at isolated stations outside of it, on the other.*

* For the names of a number of plants of pioneer tendencies which are about as common in the highlands as in the coastal plain, see Bull. Torrey Club **27**: 328 (near bottom). 1900; Torreya **5**: 56. 1905; **8**: 4–6. 1908; Plant World **9**: 226. 1907. — Kearney, Plant World **1**: 33–35. 1897; Science II. **12**: 832–836 (in part). 1900.

But, no matter how many or how few species we include in this class, present knowledge is sufficient to indicate with certainty that outside of the coastal plain their number is greatest in western Georgia and eastern Alabama, gradually decreasing northward, until in the highlands of Virginia and Kentucky there are very few such plants worth mentioning. Just why this is so is a problem to be solved in the future by the aid of geology; the object of the present paper is not to inquire into that, but to present a few additional examples recently discovered in a part of the region of greatest promise above indicated, and to indulge in a few speculations regarding their history.

One of the earliest papers dealing primarily with the exceptional occurrence of coastal plain plants farther inland is that by Mr. Kearney on the Lower Austral element in the flora of the southern Appalachian region, in Science for November 30, 1900. In Mohr's Plant Life of Alabama, published eight months later, are many details of the local distribution in that state of such species as are here discussed. Additional information about some of them can be gathered from Harbison's Sketch of the Sand Mountain Flora * and Earle's Flora of the Metamorphic Region of Alabama,† both published in the spring of 1902. In 1906 the writer published two papers ‡ giving several more instances of the same kind from northern and eastern Alabama.

Comparatively little field work has been done in those parts of the metamorphic or Piedmont region of Georgia where coastal plain plants are most likely to be found, and almost nothing has been printed about the vegetation there. In the latter part of the summer of 1908 I had occasion to spend about a month in west-

— Mohr, Contr. U. S. Nat. Herb. **6**: 60–62, 73–74, 75 (near bottom), 97. 1901. Much less was known about the details of plant distribution in the South at the beginning of this century than now, and some of the earlier discussions of geographical affinities are based on such imperfect data as to be somewhat misleading. "Austro-riparian" plants especially have been discussed at considerable length without being sufficiently defined.

* Biltmore Bot. Stud. **1**: 151–157.

† Bull. 119, Ala. Agric. Exp. Sta. In this, unfortunately few details of distribution are given, and the boundary between the metamorphic region and coastal plain is not drawn sharply enough to exclude several species which are strictly confined to the latter.

‡ Torreya **6**: 111–117; Bull. Torrey Club **33**: 523–536.

ern Middle Georgia, during which I took advantage of the opportunity to examine a good deal of territory never explored botanically before, with the not unexpected result that I found several species, most widely distributed in the coastal plain, which had not previously been seen in Middle Georgia, though nearly all were already known from upper Alabama. There is no need of apology for placing on record those which are entirely new to the known flora of the Piedmont region, and there are a few others which have been seen so few times outside of the coastal plain that they deserve to be mentioned here in order to strengthen what little evidence we already have about their distribution and habitats in these older regions. Notes on a few of the trees observed at this time have already been published in Southern Woodlands * for December, 1908.

The species which are confined to the coastal plain or nearly so are largely if not chiefly pioneer plants growing in wet places † (especially moist pine-barrens), but a few prefer dry or comparatively rich soil. The localities in Middle Georgia which yielded the most interesting results in the way of coastal plain plants last year may be briefly described as follows:

For pioneer xerophytes, the Pine Mountains stand preëminent. Some allusion has already been made to this interesting outlying range of mountains,‡ but a little further description will not be out of place here. The Pine Mountains extend from the Atlantic and Gulf divide in Pike County in a general west-southwest direction to the Chattahoochee River in Harris County, a distance of about sixty miles. They are best developed midway between the two ends, in the southern part of Meriwether County, where they are divided into several ridges, the highest rising about 1,300 feet above sea-level and 500 feet above the average of the surrounding country. These mountains are formed of sandstone (the surrounding country is granitic), and their soil is naturally rather sterile from the standpoint of the agriculturist, scarcely any crops being

* A bi-monthly magazine of forestry published at Athens, Ga. With the third volume the title was changed to *Forest, Fish and Game.*

† Conversely, those confined to the neighboring highlands are mostly climax plants preferring comparatively dry soil.

‡ Bull. Torrey Club 30: 292–294. 335. 1903; Southern Woodlands 1[3]: 13. 1907.

raised there except peaches, and those only in a few places. *Pinus palustris* is or has been abundant the whole length of the Pine Mountains (whence their name), and the flora of the summits and drier slopes has much in common with the dry pine-barrens of the coastal plain. Most of the species are of pretty wide distribution, however, and few need to be mentioned here. These mountains were visited four times in September, in Upson County on the 8th, Harris on the 12th, Pike on the 19th, and Meriwether on the 24th. Oak Mountain, in Talbot and Harris counties, is a ridge about half as high as Pine Mountain, a few miles south of it and nearly parallel to it, with similar vegetation except that the long-leaf pine seems to be absent, its place being taken by *Pinus echinata*. A few minutes were spent on the western end of this ridge near Hamilton about sunset on September 12th.

For pioneer bog or moist pine-barren plants the best places in Middle Georgia seem to be a number of bogs and meadows a few miles north of the Pine Mountains, some of which have been mentioned in a previous paper.* On September 19th last year I found another such meadow just south of Zebulon, in Pike County, and a most interesting area about four miles farther south, or half a mile north of Meansville, in the same county. Here there is a shallow, nearly level valley, with sandy soil, and tall slender specimens of *Pinus Taeda*, the only kind of tree in about 25 acres, except a few small gums (*Nyssa* and *Liquidambar*). *Pinus palustris* grows sparingly on higher ground close by, but the valley is apparently a little too moist for it. The vegetation of the low grounds (which might be called the Meansville flatwoods for convenience, as it will be referred to several times hereafter) is somewhat intermediate in character between that of low pine woods in southeastern Virginia † and that of the pine region of Limestone County, Alabama,‡ and has many species in common with both regions and with several other places where *Pinus Taeda* is the prevailing tree. Besides the more noteworthy plants to be mentioned farther on, I found at this place in passing through: — *Helianthus angustifolius*, *Sericocarpus linifolius*, *Eupatorium ver-*

* Bull. Torrey Club **30**: 294, 326. 1903.

† See Kearney, Contr. U. S. Nat. Herb. **5**: 396–405. 1901.

‡ See Torreya **6**: 115–116. 1906.

benaefolium, *E. rotundifolium*, *Viburnum nudum*, *Cephalanthus*, *Diodia virginiana*, *Cholisma ligustrina*, *Azalea viscosa*, *Ludwigia alternifolia*, *Viola primulifolia*, *Rhus copallina*, *Lespedeza angustifolia*, *Aronia arbutifolia*, *Magnolia glauca*, *Juncus aristulatus*, *J. scirpoides*, *Scleria triglomerata*, *Rynchospora glomerata*, *Scirpus Eriophorum*, *Cyperus pseudovegetus*, *Uniola laxa*, *Panicum virgatum*, *P. agrostoides*, *Pteridium aquilinum*, and a few others of similar distribution.

Species of more climax tendencies, but still chiefly confined to the coastal plain, were found in the swamps and bottoms of the Flint River and some of its larger tributaries in the southern part of Fayette County and on the borders of Spalding and Coweta adjoining, on August 22 and September 22.

The species of greatest interest observed at the localities above described are mentioned below. The most complete statements as to their known distribution up to the beginning of the present century can be found in Mohr's Plant Life of Alabama (Contr. U. S. Nat. Herb., vol. 6. 1901). In Ann. N. Y. Acad. Sci. vol. 17, part 1, I have given the latest information I had up to the summer of 1905 about the ranges of such of them as are known to occur in the Altamaha Grit region of Georgia. Specimens of several of them were collected, and such are referred to by number.

VERNONIA ANGUSTIFOLIA Michx.

In dry long-leaf pine woods on the Pine Mountains in Pike and Meriwether Counties, and among short-leaf pines on Oak Mountain in Harris County. Otherwise known only from the coastal plain.

LOBELIA GLANDULOSA Walt.

In the meadow just south of Zebulon, September 19, in bloom (*no. 2242*). Apparently never seen outside of the pine-barrens before.

OLDENLANDIA UNIFLORA L.

With the preceding. Not definitely reported outside of the coastal plain before.

AFZELIA PECTINATA (Pursh) Kuntze.

In dry woods on the northern slopes of the Pine Mountains near Warm Springs, Meriwether County. Previously known range and habitat similar to that of *Vernonia angustifolia*.

TRACHELOSPERMUM DIFFORME (Walt.) A. Gray.

On August 22 I found this evergreen vine in the Flint River swamp in Spalding County, which was not very surprising, as it had already been found farther inland in Alabama.*

SABBATIA CAMPANULATA (L.) Torr.

Abundant in the Meansville flatwoods. I had never seen this in Middle Georgia before, but Dr. Small has reported it from the mountains, † and it is known to occur at several places in the coal region of Alabama.

CYNOCTONUM SESSILIFOLIUM (Walt.) Gmel.

In 1901 I found this in a sandy bog near Molena, Pike County,‡ and last year I found it in similar situations near Zebulon, about ten miles away. No other stations seem to be known for it outside of the coastal plain, or indeed outside of the pine-barrens except near Americus, Ga.

FRAXINUS CAROLINIANA Mill.

On muddy banks of Big Potato Creek where that stream cuts through the Pine Mountains in Pike County, September 19. This is chiefly confined to the coastal plain, but Dr. Mohr has reported it from one place in northeastern Alabama,§ and Mr. C. L. Boynton from the rocky bed of a stream near Wadesboro, N. C. ||

LUDWIGIA HIRTELLA Raf.

In the sandy bog or meadow near Zebulon. Previously supposed to be confined to the coastal plain, and almost to the pine-barrens.

LUDWIGIA LINEARIS Walt.

In the Meansville flatwoods (*no. 2244*). Known range very similar to that of the preceding, except that Dr. Mohr reported it once from Lookout Mountain.

? VIOLA DENTICULOSA Pollard.

What looks more like this species than any other I am

* See Bull. Torrey Club **33** : 535. 1906.

† Bull. Torrey Club **24** : 332. 1897.

‡ See Bull. Torrey Club **30**: 294. 1903.

§ Contr. U. S. Nat. Herb. **6** : 67. 1901. (This locality is not mentioned in his catalogue of species.)

|| Biltmore Bot. Stud. **1** : 144. 1902.

acquainted with grows sparingly in the Meansville flatwoods. At the known stations for it in the coastal plain it is associated with a good many species which range as far inland as this, and there is no known reason why it should not do likewise.

TRIADENUM PETIOLATUM (Walt.) Britton.

In a creek swamp about two miles north of Zebulon, September 19. Professor F. S. Earle reports it from Tallapoosa County, Alabama (which is mostly in the metamorphic region), but with that possible exception it seems to have been known only from the coastal plain before.

ASCYRUM STANS Michx.

In the Meansville flatwoods, also in a sort of natural meadow about two miles east of Senoia, Coweta Co., which I visited on September 22. Rare at both places. I had previously seen it in Marshall and Clay counties, Alabama, but not in the Piedmont region of either state.

ILEX GLABRA (L.) A. Gray.

This is common in nearly all parts of the coastal plain in Georgia and frequent in southern Alabama, but it had apparently never been seen in the highlands of either state by a botanist until Mr. C. L. Boynton found it near Carrollton, Ga., several years ago.* Last year I found many small bushes, some with fruit, around the edges of the low pine woods or flatwoods near Meansville (*no. 2247*). I have heard some rumors of its occurrence in Coweta County also.

CYRILLA RACEMIFLORA L.

On the banks of Big Potato Creek where it cuts through the Pine Mountains in Pike County, which is probably a little farther above the fall-line than this species had ever been seen before.†

? NYMPHAEA FLUVIATILIS Harper (Bull. Torrey Club **33**: 234–236. *f. 2.* 1906).

What seems to be this species occurs in Line Creek on the

* See Ann. N. Y. Acad. Sci. **17**: 209. 1906. It cannot be very common there, for in January, 1904, I walked out from Carrollton a few miles in several different directions, bearing this species in mind, but I could not find a trace of it, though I did see a good many species which commonly associate with it.

† See Bull. Torrey Club **30**: 294. 1903.

boundary between Fayette and Coweta counties. At the time I described it I knew of no floating-leaved *Nymphaea* outside of the glaciated region and coastal plain.*

QUERCUS CATESBAEI Michx.

On dry rocky northern slopes (apparently not on the summit) of the Pine Mountains near Warm Springs, which is a few miles from where I found it in 1901. It is accompanied there usually by two related species with similar leaves, *Q. coccinea* and *Q. georgiana*, and always by *Pinus palustris*.

QUERCUS LAURIFOLIA Michx.

On sandy banks of Big Potato Creek in the Pine Mountains, Pike County. This seems to be the first station on record for this oak in Middle Georgia, but I had already found it about the same distance above the fall-line in Alabama.†

MYRICA CAROLINENSIS Mill.

Grows about four feet tall in the Meansville flatwoods (*no. 2250*). Rare in a damp ravine on the north side of the Pine Mountains between Meansville and Barnesville in the same county. Like the preceding, this had not been known to occur outside of the coastal plain in the South until I found it in upper Alabama in 1906.‡

MYRICA PUMILA (Michx.) Small.

With the preceding, about two feet tall (*no. 2251*). Dr. Mohr had reported this from Cullman County, Alabama, but otherwise it was known only in the coastal plain, and at very few places outside of the pine-barrens.

SMILAX LAURIFOLIA Walt.

In two or three branch-swamps between Zebulon and Meansville, Pike County, September 19. This too was previously unknown in Middle Georgia, but Dr. Gattinger found it long ago in East Tennessee, and the writer in 1905 on Lookout Mountain, Alabama, § and later in Randolph and Chilton counties, in the metamorphic region of the same state.

* In this connection see Rhodora **8**: 29. 1906; and the last paragraph of the original description of this species.

† See Bull. Torrey Club **33**: 529. 1906.

‡ See Bull. Torrey Club **33**: 528. 1906; **34**: 373. 1907.

§ See Torreya **6**: 114. 1906.

JUNCUS TRIGONOCARPUS Steud.

Occurs in the meadow south of Zebulon, which is not surprising, as I had found it in the adjoining county of Meriwether seven years before.

XYRIS FLEXUOSA Muhl. (*X. torta* of many authors.*)

Rather common in the Meansville flatwoods. Previously known from the coastal plain only.

CAREX GLAUCESCENS Ell.

In the swamp of the Flint River, Spalding County, and in the Meansville flatwoods; not abundant. Accompanied by *Erianthus strictus* and *Panicum agrostoides* at both places, as well as in the pine woods of Limestone County, Alabama,† which seems to be the only other locality outside of the coastal plain recorded for this *Carex*.

SCLERIA TRICHOPODA Wright.

The first sentence and half of the second, in the remarks under *Cynoctonum sessilifolium* above, will apply as well to this species.

ELEOCHARIS TUBERCULOSA (Michx.) R. & S.

Grows in the low places near Zebulon and Meansville already mentioned several times. Chiefly confined to the coastal plain, but known also from several stations in the glaciated region and mountains.‡ In 1906 I found it in the Coosa valley, in Cherokee County, Alabama.

PANICUM VERRUCOSUM Muhl.

Abundant in some parts of the Meansville flatwoods. As this ranges as far north as eastern Massachusetts, its occurrence outside of the coastal plain is not surprising.

ERIANTHUS STRICTUS Baldw.

See remarks under *Carex glaucescens*, above. The distribution of this rather rare grass is not very well understood, but it is seldom found outside of the coastal plain.

LYCOPODIUM ALOPECUROIDES L.

In the Meansville flatwoods, not abundant (*no. 2249*). Previ-

* See Torreya **5**: 129. 1905.
† See Torreya **6**: 116. 1906.
‡ See Rhodora **7**: 72. 1905; **8**: 27. 1906.

ously known only from the coastal plain, and from Henderson County in western North Carolina.*

ANCHISTEA VIRGINICA (L.) Presl.

With the preceding, more abundant (*no. 2248*). Like *Myrica carolinensis*, which grows with it, this was not known outside of the glaciated region and coastal plain until I found it in northeastern Alabama in 1906.†

To trace the history of these species which have a wide distribution in the coastal plain and are rare and local in the older regions will be one of the most fascinating problems of the phytogeography of the future. At first thought it would seem easy enough to dismiss the matter in a few words by saying that these organisms have pushed out in comparatively recent times (since the glacial period, for instance) from the regions where they are common to the scattered localities where they are rare. Up to the beginning of the present century, when Dr. Cowles brought the idea of succession of vegetation prominently before the botanists of this country, such an explanation would have seemed sufficient. Mr. Kearney in his extremely valuable and interesting paper in Science ‡ already mentioned, which was published just before what might be called the dawn of a new era of botanical investigation in America, gives scarcely a hint of succession from pioneer to climax, though he does point out that most of the species he discusses are xerophytes, growing in poor sandy soils. Even as late as the spring of 1905, the writer, not having fully grasped the idea of succession, made the suggestion, which now seems absurd, that *Pinus palustris* might have been extending its range in Middle Georgia within historic times.§

But according to the laws of succession as now understood, it is as impossible for pioneer plants to encroach on territory occupied by climax vegetation (except where the latter is weakened or destroyed by some other cause) as it is for a savage to establish himself unaided in a civilized country, or for an American farmer

* See Lloyd & Underwood, Bull. Torrey Club **27**: 157. 1900.

† See Bull. Torrey Club **33**: 523. 1906.

‡ Science II. **12**: 830–842. 1900. The author calls this "A preliminary note," but unfortunately never followed it up with anything more on the same subject.

§ Torreya **5**: 57. 1905.

or lumberman to move to Europe and continue the same occupation there. The tendency is always for climax vegetation to gain ground and pioneer vegetation to lose,* and this tendency is counteracted only by such forces as erosion, fire, and civilization. The species discussed in this paper, or the majority of them, must therefore have once been more widely distributed in the highlands than they are now; and doubtless not a few species now strictly confined to the coastal plain were more or less common farther inland in past epochs.

It is not likely that all species now endemic to the coastal plain have had such a history, however. The distribution and relationships of many of them make it seem most likely that their ancestors came in by way of Florida after the coastal plain last emerged from the sea, probably about the close of the Pleistocene period. (The Pleistocene submergence of the greater part of the coastal plain has been overlooked by nearly all botanists who have discussed the phytogeographical problems of the southeastern United States, but it is pretty generally accepted by geologists, and must have had a far-reaching effect upon the present composition of the flora.) Many species now growing in the Piedmont region have indeed near relatives in the tropics, and such (as Mr. Kearney has already suggested) probably date back to the Miocene period, when semi-tropical vegetation extended to Greenland.

After the last emergence of the coastal plain it doubtless received plant immigrants both from the north and from the south, and the present endemic coastal plain species must have been derived (by mutation or otherwise) from at least two different sources. Perhaps in the not distant future it will be possible to separate them all into two or more classes on this basis.

COLLEGE POINT, N. Y.

*See Bull. Torrey Club 33: 529, 531. 1906; 34: 373. 1907; Southern Woodlands 1[3]: 8–9. 1907.

Studies in the North American Convolvulaceae — V. Quamoclit

Homer Doliver House

The genus *Quamoclit* dates back to Tournefort, but was merged by Linnaeus into *Ipomoea*. The type of the Tournefortian genus *Quamoclit* is the species herein recognized under the name of *Quamoclit pinnata* (Desr.) Boj. (*Quamoclit Quamoclit* Britton). This species is by priority of citation the technical type of *Ipomoea* and in restoring *Quamoclit* to generic rank, Moench unfortunately takes up only *Ipomoea coccinea* in the genus, but credits the genus to Tournefort.

The writer has already expressed his opinion regarding the validity of *Quamoclit* and *Ipomoea* (Ann. N. Y. Acad. Sci. **18**: 181. 1908), and proceeds here to maintain the genus *Quamoclit* in the sense typified by the Tournefortian type, and recognized under the name of *Quamoclit* in all subsequent literature wherever *Ipomoea Quamoclit* of Linnaeus is not regarded as congeneric with the species usually placed in *Ipomoea*.

Quamoclit Moench, Meth. 453. 1794

Calboa Cav. Ic. **5**: 51. 1799.
Macrostemma Pers. Syn. **1**: 185. 1805.
Mina Llav. & Lex. Nov. Veg. Descr. **1**: 3. 1824.
Morenoa Llav. & Lex. *loc. cit.* 5.
Doxema Raf. Fl. Tellur. **4**: 75. 1838.
Neorthosis Raf. *loc. cit.* 125.

Annual or perennial, twining, mostly herbaceous vines. Leaves alternate; blades entire, lobed or divided. Flowers in axillary usually 2-forked, few- or many-flowered clusters. Sepals 5, membranaceous or herbaceous, equal or nearly so, often awned at or near the apex with straight or recurved appendages. Corolla small or medium-sized, the tube not expanding at the base, the limb subsalverform, cup-shaped or rarely funnelform, usually more or less lobed. Stamens 5, with the style exserted and usually conspicuously declinate; filaments filiform. Ovary 2-celled, ovules 4; stigma capitate. Capsules subglobose or somewhat elongated, the style often persistent in fruit. Seeds smooth.

TYPE SPECIES: *Quamoclit pinnata* (Desr.) Boj. (*Ipomoea Quamoclit* L., *Quamoclit vulgaris* Choisy).

Key to the North American species

Sepals without awns; leaves pinnately divided; pedicels thickened; corolla-tube clavate. (Section *Euquamoclit* Peter.) 1. *Q. pinnata.*

Sepals awned; leaves entire or lobed. Corolla-limb shorter than the tube. (Section *Calboa* Peter.)

Corolla-limb expanding abruptly from a slender tube, the limb campanulate or cup-shaped.

Limb of the corolla deeply campanulate, deeply lobed.

Lobes of the corolla-limb rounded.

Corolla red or scarlet, the tube about 3–4 cm. long..... 2. *Q. Lindleyi.*

Corolla yellow, the tube about 2 cm. long..... 3. *Q. Langlassei.*

Lobes of the corolla-limb oblong-lanceolate, acute; tube about 1.5 cm. long; corolla yellowish, tinged with purple..... 4. *Q. globosa.*

Corolla-limb shallowly cup-shaped, about 1.5 cm. broad, angulately lobed, the tube 3–5 cm. long..... 5. *Q. coccinea.*

Corolla-limb expanding funnelform or tubular from a slender and often bent tube.

Corolla-limb 5-angled, about 1.5 cm. broad, the tube fully 5 cm. long..... 6. *Q. grandiflora.*

Corolla-limb deeply 5-lobed, lobes acute; the tube about 3 cm. long..... 7. *Q. vitifolia.*

Corolla-limb cylindrical and bent, longer than the tube, yellow, tinged with red. (Section *Mina* House.)..... 8. *Q. lobata.*

1. QUAMOCLIT PINNATA (Desr.) Boj. Hort. Maurit. 224. 1837

Ipomoea Quamoclit L. Sp. Pl. 159. 1753.

Convolvulus pennatus Desr. in Lam. Encyc. **3**: 567. 1789.

Convolvulus pennatifolius Salisb. Prodr. 124. 1796.

Convolvulus Quamoclit Spreng. Syst. **1**: 591. 1825.

Quamoclit vulgaris Choisy, Mém. Soc. Phys. Genèv. **6**: 434. 1833.

Ipomoea cyamoclita St. Lag. Ann. Soc. Bot. Lyon **7**: 128. 1880.

Quamoclit Quamoclit Britton; Britton & Brown, Illust. Fl. **3**: 22. 1898.

Stems several m. long, glabrous: leaf-blades 2–10 cm. long, the pinnate segments narrowly linear; petioles shorter than the blades with numerous short leafy branches in their axils appearing stipule-like: peduncles commonly longer than the leaves; pedicels 25–30 mm. long, thickened and fleshy at least in fruit: sepals oblong, obtuse, mucronate, 3–5 mm. long: corolla scarlet or

white, 25–35 mm. long, the tube clavate, the limb nearly flat, the short ovate lobes acute: capsules ovoid, 4-celled, 8–10 mm. high.

TYPE LOCALITY: India.

DISTRIBUTION: Circumtropical and extended by cultivation and as an escape throughout the southern United States, north to Virginia and Kansas.

ILLUSTRATIONS: Rumph. Amb. *pl. 155. f. 2.* — Tourn. Inst. *pl. 39.* — Rheede, Mal. **11**: *pl. 60.* — Bot. Mag. *pl. 188*, *pl. 244.* — Britton & Brown, *loc. cit. f. 2944.* — Bailey, Cyclop. Am. Hort. *f. 1166.*

2. **Quamoclit Lindleyi** nom. nov.

Calboa globosa Lindl. Jour. Hort. Soc. **5**: 82. 1850. Not *Morenoa globosa* Llav. & Lex. 1824, or *Quamoclit globosa* G. Don, 1838.

Perennial, twining, glabrous: leaf-blades ovate, usually 3–5-lobed, lobes lanceolate, entire, acute or some of the blades merely angulate or dentate, and cordate-hastate at the base; petioles longer than the blades: peduncles exceeding the subtending leaves, 25–35 cm. long, 3–9-flowered; pedicels filiform, 3–10 cm. long: sepals ovate, blunt, the infraterminal awns 6–8 mm. long: corolla deep red, 5–6 cm. long, the cylindrical tube about as long as the deep cup-shaped limb, the lobes of the limb broad and rounded with wavy crenulate margins: capsules about 10 mm. high.

TYPE LOCALITY: Guatemala.

DISTRIBUTION: Southern Mexico and Central America.

ILLUSTRATIONS: Lindl. *loc. cit.* (text fig.).

SPECIMENS EXAMINED: Guanajuato: *A. Duges*, 1880 (Gray Herb.). Oaxaca: Cuyamecalco, *L. C. Smith 604*, 1895 (Gray Herb.).

3. **Quamoclit Langlassei** sp. nov.

Perennial, twining, glabrous: leaf-blades oblong-ovate, 8–10 cm. long, cordate-hastate and fiddle-shaped, the basal auricles spreading, rounded or obtuse, often with lateral acuminations, about 4 cm. broad at the base, constricted above, the apex abruptly acute; petioles 3–4 cm. long: peduncles elongated, 20 cm. long or longer, few-flowered; pedicels slender, about 2 cm. long: sepals oblong, somewhat unequal, obtuse or rounded, the infraterminal awns 8–10 mm. long: corolla bright yellow, 3.5–4 cm.

long, the tube about 2 cm. long and bent, the limb campanulate, fully 3 cm. broad with 5 rounded lobes: style persistent in fruit.

"Crète de la Sierra Madre" (southern Mexico). Plants of Michoacan & Guerrero, 2250 m. alt., *E. Langlassé 875*, Nov. 16, 1899. Type, sheet *no. 386,249* in the U. S. National Herbarium.

4. QUAMOCLIT GLOBOSA (Llav. & Lex.) G. Don, Gen. Syst. **4**: 259. 1838. — Benth. Pl. Hartw. 89. 1839

Morenoa globosa Llav. & Lex. Nov. Veg. Descr. **1**: 5. 1824.

Ipomoea globosa Meissn. in Mart. Fl. Bras. **7**: 220. 1869. (Excl. syn. Lindl., Cav., and Choisy.)

Ipomoea Hartwegii Meissn. *loc. cit.* Not *Ipomoea Hartwegi* Benth. 1839.

Perennial, twining, glabrous: leaf-blades ovate, cordate, deeply 3–5-lobed, 10–15 cm. long, lobes acute or acuminate, the middle lobe largest, ovate, scarcely or not at all constricted at the base, lateral lobes obliquely triangular, their outer margins usually with 1–3 sharp teeth; petioles usually longer than the blades: peduncles exceeding the subtending petioles and usually the blades, 15–25 cm. long, stout; pedicels filiform, 1–2 cm. long: sepals ovate or oval, 3–4 mm. long, the awns 2–3 mm. long: corolla 2.5–3 cm. long, erect, yellowish, the tube one third as long, cylindrical and bent, ventricosely dilated above into a subglobose or deeply campanulate limb, throat and base of the tube tinged with purple, the 5 short ovate obtuse lobes erect or spreading: capsules ovoid, 4–5 mm. high.

TYPE LOCALITY: San José del Corral, Mexico.

DISTRIBUTION: Southern Mexico to Brazil.

SPECIMENS EXAMINED: Mexico: Colipa, *Karwinsky 598*, 1841; Colima, *Palmer 1104*, 1891. Guatemala: Aceituna, *J. D. Smith 1874*, 1890. Salvador: *Carlos Renson 82*.

5. QUAMOCLIT COCCINEA (L.) Moench, Meth. 453. 1794

Ipomoea coccinea L. Sp. Pl. 160. 1753.

Ipomoea angularis Willd. Nov. Act. Cur. **4**: 197. 1770.

Convolvulus coccineus Salisb. Prodr. 124. 1796.

Ipomoea acuminata Ruiz & Pav. Fl. Per. **2**: 11. 1799.

Ipomoea angulata Ruiz & Pav. *loc. cit.*

Ipomoea cholulensis H.B.K. Nov. Gen. et Sp. **3**: 112. 1819.

Ipomoea dichotoma H.B.K. *loc. cit.*
Ipomoea phoenicea Roxb. Hort. Beng. 14. 1814. Fl. Ind. **1**: 502. 1832.
Convolvulus acutangularis Spreng. Syst. **1**: 599. 1825.
Convolvulus indivisus Vell. Fl. Flum. **2**: *pl. 50.* 1827.
Quamoclit cholulensis G. Don, Gen. Syst. **4**: 259. 1838.
Quamoclit Ruiziana G. Don, *loc. cit.* 258.
Quamoclit dichotoma G. Don, *loc. cit.* 259.
Ipomoea erythraea Moc. & Sessé; Choisy, in DC. Prodr. **9**: 335. 1845.
Ipomoea parviflora Sessé & Moc., Fl. Mex. 42. 1893.
Quamoclit indivisa Hallier f. Bot. Jahrb. **25**: 5. 1898.

Annual, twining, glabrous: stems several m. long: leaf-blades ovate, 3–10 cm. long, cordate, acute or acuminate at the apex, usually thin and submembranaceous, pale beneath, entire or somewhat hastate or angulately lobed; petioles as long as the blades or shorter: peduncles about equaling the leaves or longer, few-flowered or sometimes many-flowered: sepals oblong, 4–6 mm. long, the outer ones with subulate, infraterminal awns 2–5 mm. long: corolla scarlet, white or orange, the tube 3–4 cm. long, slightly enlarged above, the shallowly cup-shaped limb 1.5–2 cm. broad, 5-angled: capsules globose, 6–7 mm. high.

TYPE LOCALITY: St. Domingo.

DISTRIBUTION: Circumtropical. In America north to Florida, Texas, and Arizona. Extended as an escape from cultivation to Pennsylvania, Ohio, Missouri, and Arkansas.

ILLUSTRATION: Jacq. Ic. Pl. Rar. **1**: *pl. 35.* — Bot. Repos. *pl. 499.* — Bot. Mag. *pl. 221.* — Ruiz & Pav. *loc. cit. pl. 120. f. b.* — Naves, in Blanco, Fl. Filipp. Ic. **2**: *pl. 17.* — Bailey, Cyclop. Am. Hort. *f. 1168.* — Britton & Brown, Illust. Fl. **3**: *f. 2945.*

QUAMOCLIT COCCINEA HEDERIFOLIA (L.) House, Ann. N. Y. Acad. Sci. **18**: 262. 1908

Ipomoea hederifolia L. Syst. ed. 10, 925. 1759.
Ipomoea sanguinea Vahl, Symb. Bot. **3**: *pl. 33.* 1794.
Ipomoea hastigera H.B.K. Nov. Gen. et Sp. **3**: 111. 1819.
Ipomoea Humboldtiana Roem. & Schult. Syst. **4**: 789. 1819.
Convolvulus hederifolius Spreng. Syst. **1**: 594. 1825.
Convolvulus sanguineus Spreng. *loc. cit.*

Convolvulus hastigerus Spreng. *loc. cit.*

Quamoclit hastigera G. Don, Gen. Syst. **4**: 259. 1838.

Quamoclit hederifolia Choisy, in DC. Prodr. **9**: 336. 1845.

Quamoclit russelliaefolia Mart. & Gal. Bull. Acad. Brux. **12**: 271. 1845.

Ipomoea coccinea var. *hederifolia* A. Gray, Syn. Fl. N. Am. 2^1: 209. 1878.

Quamoclit gracilis Hallier f. Bull. Herb. Boiss. **7**: 416. 1899.

Quamoclit brevipedicellata Hallier f. *loc. cit.*

Similar to the type in size and habit: leaf-blades deeply 3-lobed, lobes, especially the middle, narrowed at the base, lateral lobes angulate-dentate or lobed on the outer margins.

TYPE LOCALITY: America.

DISTRIBUTION: Texas, New Mexico, and Arizona, throughout tropical America.

ILLUSTRATIONS: Plum. Am. *pl. 93. f. 2.* — Vahl, *loc. cit. pl. 33.* — Bot. Reg. *pl. 9.* — Bot. Mag. *pl. 1769.* — Bailey, Cyclop. Am. Hort. *f. 1169.*

QUAMOCLIT COCCINEA PUBESCENS (Cham. & Schlecht.) Choisy, in DC. Prodr. **9**: 335. 1845

Ipomea coccinea var. *pubescens* Cham. & Schlecht. Linnaea **5**: 118. 1830.

Leaf-blades usually entire, or the basal auricles of the cordate-hastate blades angulately toothed, thick and firm in texture, softly and densely appressed-pubescent.

TYPE LOCALITY: Hacienda de la Laguna, prope Palapam, Mexico.

DISTRIBUTION: Southern Mexico and Guatemala.

Quamoclit coccinea luteola (Jacq.) comb. nov.

Ipomea luteola Jacq. Ic. Pl. Rar. **1**: *pl. 35.* 1781–86.

Ipomea coccinea β Willd. Sp. Pl. **1**: 880. 1798.

Convolvulus luteolus Spreng. Syst. **1**: 599. 1825.

Ipomea coccinea var. *luteola* Meissn. in Mart. Fl. Bras. **7**: 218. 1869.

Quamoclit lutea Hemsley, Biol. Cent.-Am. Bot. **2**: 389. 1882.

Merging into *Q. coccinea*, but in its typical form somewhat larger and stouter than the type: petioles longer than the blades:

sepals ovate, 4–7 mm. long, the awns 4–8 mm. long: corolla yellow, the tube bent and somewhat contracted at the throat, 4–5 cm. long.

TYPE LOCALITY: St. Domingo.

DISTRIBUTION: Tropical America.

ILLUSTRATIONS: Jacq. Ic. Pl. Rar. *pl. 35.* — Hemsley *loc. cit. pl. 60.*

Quamoclit coccinea jaliscana var. nov.

Glabrous: leaf-blades rather thick and firm in texture, oblong-lanceolate, usually attenuate or long-acuminate at the apex, 5–10 cm. long, 3–4 cm. broad, the base cordate-sagittate or subtruncate, the basal auricles obtusely angled: sepals equal, about 5 mm. long, the awns only 2–4 mm. long: corolla scarlet.

MEXICO: Between San Sebastian and summit of Mt. Bufa de Mascota, 4800 ft. alt., Jalisco, *E. W. Nelson 4094*, 1897. Type, sheet *no. 327,133* in the U. S. National Herbarium.

6. QUAMOCLIT GRANDIFLORA (Llav. & Lex.) G. Don, Gen. Syst. **4**: 259. 1838

Morenoa grandiflora Llav. & Lex. Nov. Veg. Descr. **1**: 17. 1824.
Ipomoea Funis Cham. & Schlecht. Linnaea **5**: 118. 1830.
Ipomoea Llaveana Meissn. in Mart. Fl. Bras. **7**: 219. 1869.

Perennial, twining, somewhat woody below: leaf-blades ovate, 6–15 cm. long, cordate or cordate-hastate, 3-lobed, acuminate, the sides of the lateral lobes angular or toothed, finely pubescent beneath on the veins, younger parts finely pubescent, otherwise glabrous; petioles as long as the blades or longer: peduncles much exceeding the subtending leaves, 30–40 cm. long, 3–9-flowered; pedicels filiform, 1–3 cm. long; sepals ovate-lanceolate or suborbicular, 3–5 cm. long, the awns as long: corolla scarlet, about 5 cm. long, the tube slender, bent, expanding above into a 5-angled limb about 2 cm. broad: capsules 10 mm. in diameter or less.

TYPE LOCALITY: Near Jalapa and San Andres, Mexico.

DISTRIBUTION: Southern Mexico and Central America.

ILLUSTRATIONS: Cham. & Schlecht. *loc. cit.*

SPECIMENS EXAMINED: Prope Jalapa et San Andres, *Schiede 228, 556*, 1828. Orizaba, *Müller 1869*, 1853; *Vischer*, 1838. Chiapas: Chicharras, *E. W. Nelson 3768*, 1896 (Gray Herb.); between Teneapa and Yajalon, 3000–5000 ft. alt., *E. W. Nelson 3297*, 1895 (Gray Herb.).

7. QUAMOCLIT VITIFOLIA (Cav.) G. Don, Gen. Syst. **4**: 259. 1838

Calboa vitifolia Cav. Ic. **5**: 51. 1799.
Macrostemma vitifolia Pers. Syn. **1**: 185. 1805.
Convolvulus Neei Spreng. Syst. **1**: 593. 1825.
Ipomoea peduncularis Bertol. Fl. Guatem. 8. 1840.
Exogonium umbellatum Moc. & Sessé; Choisy, in DC. Prodr. **9**: 336. 1845.

Perennial, twining, glabrous: leaf-blades ovate, 8–15 cm. long, cordate or cordate-sagittate, entire or usually 3-lobed, lobes ovate or oblong-lanceolate, acuminate, the middle lobe constricted below; petioles usually longer than the blades: peduncles exceeding the subtending leaves, 25–40 cm. long, 3–many-flowered: sepals ovate or suborbicular, 4–5 mm. long, the infraterminal awns as long: corolla 3.5–4 cm. long, the tube cylindrical, yellowish, slender, somewhat expanded toward the top, the limb scarlet, 2–2.5 cm. broad, deeply 5-lobed, the lobes lanceolate or oblong-lanceolate, acute, the exserted stamens elongated and declinate.

TYPE LOCALITY: Near Santa Blas, Mexico.

DISTRIBUTION: Southern Mexico and Central America.

ILLUSTRATIONS: Cav. Ic. **5**: *pl. 476.* — Bertol. *loc. cit. pl. 2.*

SPECIMENS EXAMINED: Tres Marias Islands: Maria Madre, *Nelson 91, 4235*, 1897. Sinaloa: Esquinapa, *Lamb 501*, 1895. Michoacan: near Los Reyes, *E. W. Nelson 6850*, 1903. Guerrero: Sierra Madre, *Langlassé 810*, 1899. Guatemala: Santa Rosa, *Heyde & Lux 4349*, 1892; between Rodes and Malacate, *E. W. Nelson 3733*, 1896.

8. **Quamoclit lobata** (Llav. & Lex.) comb. nov.

Mina lobata Llav. & Lex, Nov. Veg. Descr. 3. 1824.
Quamoclit Mina G. Don, Gen. Syst. **4**: 259. 1838.
Ipomoea versicolor Meissn. in Mart. Fl. Bras. **7**: 220. 1869.

Perennial, slender and twining, herbaceous above: leaf-blades ovate, deeply cordate, deeply 3-lobed, the middle lobe constricted below, the lateral lobes often again lobed: peduncles much longer than the subtending leaves, 30–40 cm. long, dichotomously several-flowered, the flowers somewhat secund on the two main branches of the inflorescence: sepals equal, 3–4 mm. long, the awns recurved: corolla yellow, tinged above with red or scarlet, the tube shorter than the limb, only 5–6 mm. long and about 2

mm. in diameter, almost wholly included in the calyx; the limb cylindrical or flask-shaped, about 2 cm. long and 1 cm. in diameter, bent, the stamens and style declinate against the upper side of the limb, their tips recurved along the lower side in bud, long-exserted when the limb expands, margin of limb somewhat constricted, with 5 small, acute lobes.

TYPE LOCALITY: Mexico.

DISTRIBUTION: San Luis Potosi to Central and South America.

ILLUSTRATIONS: Bot. Reg. *pl. 24.* — Paxt. Bot. Mag. **14**: 100. — Morren, Ann. Soc. Agric. Gand **5**: *pl. 259.*

SPECIMENS EXAMINED: San Luis Potosi; *Schaffner 111, 355,* 1897.

NEW YORK BOTANICAL GARDEN.

Two new spermatophytes from California

ERNEST A. MCGREGOR

Oxytheca Abramsii sp. nov.

Acaulescent or nearly so, 7–18 cm. high or less, sparingly dichotomously branched: stems glabrous mostly, but glandular just above the axils, herbaceous, becoming later more wiry: leaves spatulate, gradually narrowed to a wide petiole, 1.25–3 cm. long, scabrous-margined and the midvein slightly scabrous beneath; bracts ternate, slightly unequal, mucronate, ovate-lanceolate, connate and deflected mainly to one side, 3 mm. long: involucres broadly obconical, on peduncles 1–1.5 cm. long, those from the main axils rarely 2.5 cm. long; involucre-tube 1.5–2 mm. high; awns 10 (rarely 12), very fine, weak, but straight, 4 mm. long or less, the interval between the involucral ribs much wider than the ribs: flowers 6–8, at length nearly equaling the awns; pedicels equaling the perianth, well exserted from the involucre-tube: perianth about 4 mm. broad, cleft to base, lobes equal, elliptical, 2 mm. long, white or pinkish with wine-red midvein, slightly glandular and scabrous beneath: stamens inserted on perianth at base, shorter than the segments: styles 3, capitate: ovary glabrous.

O. Abramsii is nearest to *O. Parishii*, from which it differs in the following characters:

O. Parishii: Involucral ribs very prominent, firm, with the intervals almost lacking; awns 18–20, 3 times length of tube, strong, stiff, wiry; umbels 5–14-flowered; stems pale-glaucous, wiry.

O. Abramsii: Involucral ribs barely discernible, with intervals much wider than ribs; awns usually 10, not greatly exceeding the tube, inclined to be weak and herbaceous, though straight; umbels 6–8-flowered; stems green or reddish, not wiry.

Topatopa Mountains, Ventura Co., California. Growing on slopes in loose shale, elev. 1700 m. Collected by Abrams & McGregor (*no. 72*), June 5, 1908.

Malacothrix arachnoidea sp. nov.

Perennial herb, with stout, freely branching, and very leafy herbaceous stem, 4.5–6 dm. high; herbage hoary throughout with

a dense woolly pubescence: leaves broadly lanceolate to linear-lanceolate, attenuate above, apiculate, tapering gradually below but sessile, and never at all auriculate or clasping, entire, or the

FIGURE 1. *Oxytheca Abramsii* McGregor. Natural size.

lower rarely remotely and obscurely dentate, 4–9 cm. long, reduced upward: heads terminating numerous branches, many-flowered; involucre 13–15 mm. high, hemispherical; bracts in about two series, becoming somewhat glabrate, the inner linear-lanceolate, acuminate, the outer similar but narrower and half as long; calyculate scales few: corolla white or pinkish; ligule 10 mm. long; tube 6 mm. long, puberulent on its upper third: achenes (not matured) broadly obovate-oblong, apparently 10-ribbed, the slightly contracted summit bearing a well-expanded crown whose rim is merely crenulate; pappus-bristles snow-white, all falling together.

Carmel Valley, Monterey Co., California; by the roadside. Collected by the writer (*no. 1575*), July 1, 1906.

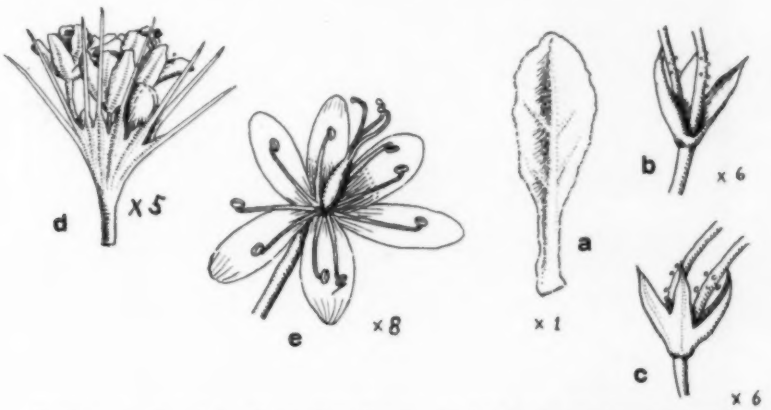

Figure 2. *Oxytheca Abramsii* McGregor; *a*, leaf, natural size; *b*, bract, from free side, × 6; *c*, bract, from deflected side, × 6; *d*, involucre, showing ribs, awns, and flowers, × 5; *e*, flower laid open to show parts, × 8.

This plant belongs to the *M. saxatilis* group, which includes *M. saxatilis* (Nutt.) Torr. & Gray, *M. tenuifolia* (Nutt.) Torr. & Gray, *M. altissima* Greene, and *M. implicata* Eastw.

On the whole these species are very closely related and form a very natural group, differing from the other members of the genus in the following characters: tall, leafy perennials; involucral scales in two appressed equal series; receptacle with no bristles; no persistent pappus-bristles. It would seem that they might well constitute at least a valid subgenus.

The characters of the flower and those of the achene of the different species are much alike, the important differences being

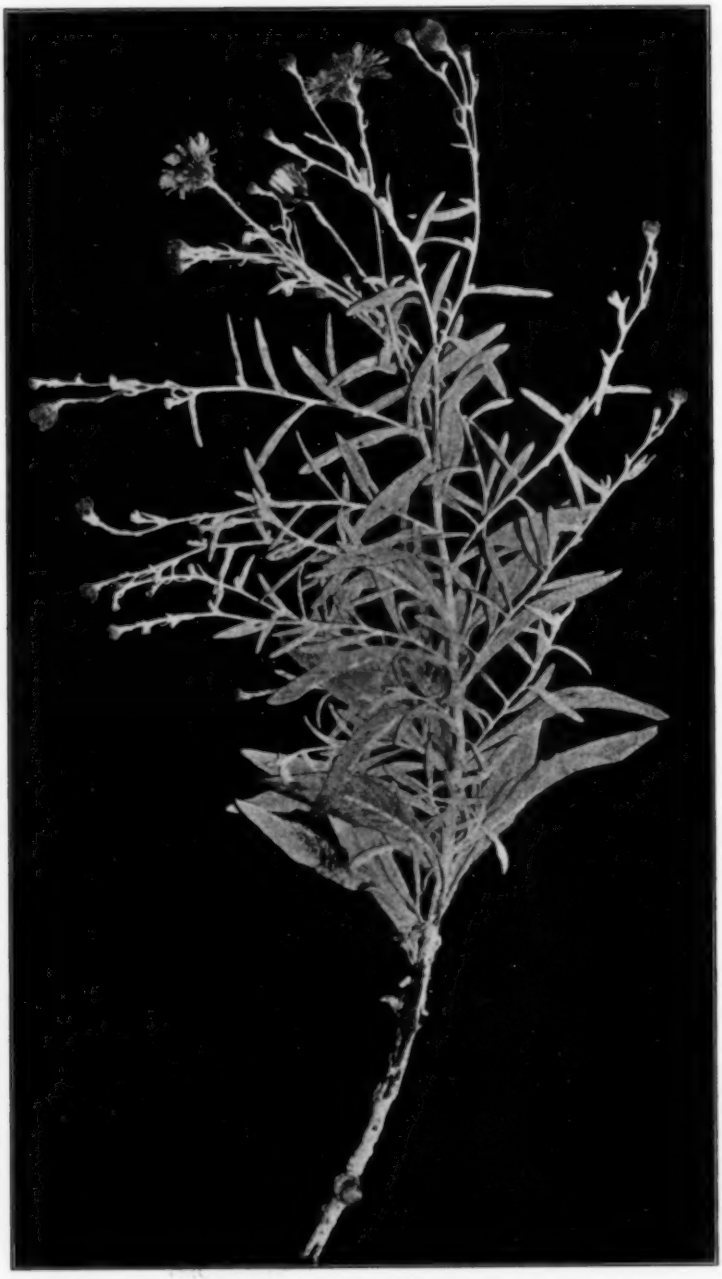

FIGURE 3. *Malacothrix arachnoidea* McGregor. One half natural size.

in the aspect of the plants and the form of the leaves which, for a given type, seem quite distinctive.

Malacothrix arachnoidea is nearest to *M. saxatilis*, from which it is to be distinguished as follows:

M. saxatilis: Green, often woolly on young parts; leaves obtuse, lower occasionally pinnatifid, auriculate, and partly clasping toward the base; calyculate scales very numerous; achenes crowned with a denticulate border.

M. arachnoidea: Hoary throughout with a dense woolly pubescence; leaves apiculate-acute, apparently never pinnatifid, auriculate, or clasping; the well-expanded crown of the achene with a merely crenulate border.

Leland Stanford Junior University.

INDEX TO AMERICAN BOTANICAL LITERATURE

(1909)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in its broadest sense.

Reviews, and papers which relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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